

The Neuroscientist

<http://nro.sagepub.com/>

The Importance of Social Rewards and Social Networks in the Human Brain

Dominic S. Fareri and Mauricio R. Delgado

Neuroscientist published online 21 February 2014

DOI: 10.1177/1073858414521869

The online version of this article can be found at:

<http://nro.sagepub.com/content/early/2014/02/21/1073858414521869>

Published by:



<http://www.sagepublications.com>

Additional services and information for *The Neuroscientist* can be found at:

Email Alerts: <http://nro.sagepub.com/cgi/alerts>

Subscriptions: <http://nro.sagepub.com/subscriptions>

Reprints: <http://www.sagepub.com/journalsReprints.nav>

Permissions: <http://www.sagepub.com/journalsPermissions.nav>

>> [OnlineFirst Version of Record](#) - Feb 21, 2014

[What is This?](#)

The Importance of Social Rewards and Social Networks in the Human Brain

The Neuroscientist
1–16
© The Author(s) 2014
Reprints and permissions:
sagepub.com/journalsPermissions.nav
DOI: 10.1177/1073858414521869
nro.sagepub.com



Dominic S. Fareri¹ and Mauricio R. Delgado²

Abstract

The rapid development of social media and social networking sites in human society within the past decade has brought about an increased focus on the value of social relationships and being connected with others. Research suggests that we pursue socially valued or rewarding outcomes—approval, acceptance, reciprocity—as a means toward learning about others and fulfilling social needs of forming meaningful relationships. Focusing largely on recent advances in the human neuroimaging literature, we review findings highlighting the neural circuitry and processes that underlie pursuit of valued rewarding outcomes across non-social and social domains. We additionally discuss emerging human neuroimaging evidence supporting the idea that social rewards provide a gateway to establishing relationships and forming social networks. Characterizing the link between social network, brain, and behavior can potentially identify contributing factors to maladaptive influences on decision making within social situations.

Keywords

reward, striatum, medial prefrontal cortex, social network, fMRI

Introduction

We live in an increasingly interconnected world. Recent technological advances in communication and interaction, from video calls to the rampant use of social media (e.g., Twitter) and social network sites (e.g., Facebook) offer the opportunity to be virtually connected with others at will. Recent estimates indicate an active monthly Facebook user database of 1.15 billion users and an active daily Facebook user database of almost 700 million (<http://newsroom.fb.com/Key-Facts>). These numbers powerfully illustrate the importance placed on social networks in modern human society. The significance of forming social groups (Axelrod and Hamilton 1981; Rand and others 2011) and long-standing close relationships (Dunbar 2012) is not necessarily surprising and may represent an evolutionarily conserved phenomenon. However, their increased prevalence in our society today begs the question of what makes a social network so compelling? Is there something about being part of a network or group that signifies some value to us? Are we motivated to pursue connections with others so as to satisfy some need that is related to our survival or well-being, similarly to other biologically relevant goals or rewards (e.g., food, sex)?

Behavior across species is at its core goal-directed, motivated in large part by positive outcomes—for example, rewards—that confer benefits and aid survival. Food, money, and sex are all powerful rewards that carry

significance (i.e., value) not only because they can provide pleasure, but because they also satisfy biologically relevant needs. An extensive literature exists highlighting neural mechanisms involved in pursuit and valuation of these types of non-social rewards (Delgado 2007; Haber and Knutson 2010; O’Doherty 2004). However, social needs are equally relevant and motivating forces for behavior. Indeed, research in recent years has converged on the notion that socially relevant rewards may be represented in neural circuitry overlapping with that for non-social rewards (Bhanji and Delgado 2014), highlighting their motivational relevance. For instance, the pursuit of other’s approval and acceptance may reflect the desire to fulfill social needs, underlying the importance placed on forming relationships and social networks (Baumeister and Leary 1995; van Winden and others 2008).

Our day-to-day experiences often occur within some social context—for example, collaborating with colleagues in the workplace—and involve members of our social networks. While our social networks can be comprised of members with whom we share varying degrees

¹Department of Psychology, University of California, Los Angeles, CA, USA

²Department of Psychology, Rutgers University, Newark, NJ, USA

Corresponding Author:

Dominic S. Fareri, Department of Psychology, University of California, Los Angeles, Franz Hall, Room 2258B, Los Angeles, CA 90025, USA.
Email: dfareri@ucla.edu

of closeness, repeated interactions occur most frequently with those people whom we have established close relationships (e.g., close friends, family members). The social context created by close, in-network relationships can influence not only our subjective daily experiences, but decision-making behavior as well. Establishing links between social network, underlying neural structure and function, and social decision making is an exciting new frontier in social neuroscience with the potential to uniquely delineate mechanisms underlying social behavior.

This review will characterize neural mechanisms supporting reward-related behavior across non-social (e.g., pursuing rewards in an isolated manner for oneself, or in the context of a non-social entity) and social contexts (e.g., pursuing rewards in the context of others), with the goal of highlighting the importance of social relationships on motivated social behavior. We will first outline neural structures comprising a circuit involved in valuation of non-social rewards that are important for basic biological survival across species. Next, we will discuss differential functional roles of some components of this putative reward circuit. We will focus largely on human studies employing functional magnetic resonance imaging (fMRI) in conjunction with behavioral methods, which have highlighted significant roles for the striatum and regions of prefrontal cortex. Third, we will review the role of reward circuitry in coding the value of social rewards and in supporting behavior during social interactions. Finally, we will examine emerging evidence characterizing the relationship between social network, brain and behavior, with a specific focus on the interplay between social network and neural regions involved in reward valuation.

Neural Structures Supporting Reward Processing

The importance of functional neural loops between areas of prefrontal cortex and the basal ganglia (see Fig. 1) to reward processing and goal-directed behavior has been demonstrated across species (Haber and Knutson 2010; Robbins and Everitt 1996; Sesack and Grace 2010). Though traditionally thought to be a structure primarily involved in motor function, the basal ganglia shares extensive connectivity with cortical and subcortical regions involved in executive function and affective processes (Haber and Knutson 2010; Middleton and Strick 2000a; Robbins and Everitt 1996; Sesack and Grace 2010). This suggests a potentially broader role for the basal ganglia. The striatum is a particularly important component to consider, as it is the primary input unit to the basal ganglia, receiving afferent projections from

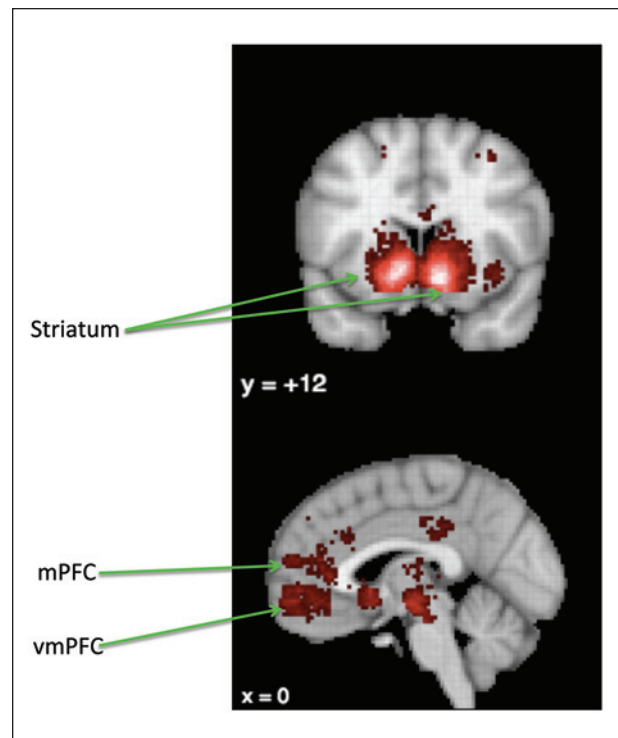


Figure 1. A meta-analysis of 329 studies using Neurosynth (Yarkoni and others 2011). Depicted here is a “Reward” reverse inference map (i.e., $p[\text{reward}|\text{activation}]$), which indicates the likelihood that studies reporting blood oxygen level-dependent (BOLD) activation in highlighted regions use the term “Reward.” As can be observed, this analysis reveals robust activation in putative reward circuitry. Highlighted here are clusters in the bilateral dorsal and ventral striatum, medial prefrontal cortex (mPFC), including anterior cingulate cortex (ACC) and ventromedial prefrontal cortex (vmPFC). Maps false discovery rate corrected at $q < .05$, $z < 2.3$.

numerous areas (Haber and Knutson 2010; Middleton and Strick 2000a). We will focus primarily on the roles of the striatum and medial prefrontal cortex in this review, given their extensive roles in supporting reward-related and social processing.

The striatum receives input from prefrontal cortical regions as well as from subcortical nuclei, and is commonly subdivided into dorsal and ventral components (Middleton and Strick 2000a; Robbins and others 1989; Robbins and Everitt 1996; Voorn and others 2004). Cognitive and motor aspects of reward processing are often associated with the dorsal striatum—the caudate nucleus and putamen—and are facilitated by afferents from primary motor cortex, dorsolateral prefrontal cortex (PFC) and medial PFC (mPFC) (Alexander and others 1986; Middleton and Strick 2000b). Connections with mPFC may specifically contribute to learning action–outcome pairings (Delgado 2007; Haber and

Knutson 2010; O'Doherty 2004; Ostlund and Balleine 2005; Pennartz and others 2011). More commonly associated with hedonic aspects of reward processing (e.g., reward seeking/consumption) and computing learning signals to aid in the association of reward outcome prediction is the ventral striatum—the nucleus accumbens (NAcc) and ventral parts of the caudate and putamen (Haber and Knutson 2010; Pennartz and others 2011; Robbins and others 1989; Robbins and Everitt 1996). The ventral striatum receives afferents from neural regions more traditionally implicated in affective processes, including orbitofrontal cortex (OFC), dorsal anterior cingulate cortex, ventromedial PFC, the amygdala, and hippocampus (Groenewegen and others 1999; Haber and Knutson 2010; Ostlund and Balleine 2007; Pennartz and others 2011; Robbins and Everitt 1996; Sesack and Grace 2010). Important reciprocal connections exist between the ventral striatum and midbrain dopaminergic nuclei (Haber and others 2000; Haber and Knutson 2010; Middleton and Strick 2000a; Robbins and Everitt 1996; Sesack and Grace 2010), allowing for dopaminergic influence on ventral striatal activity which may support reward valuation and learning (Haber and Knutson 2010; Middleton and Strick 2000a; Schultz 1997; Sesack and Grace 2010). Given its extensive connectivity, the striatum can play an important role in integrating both cognitive and affective signals central to reward valuation and learning.

Functional Contributions of Striatum and Prefrontal Cortex to Reward Valuation

The striatum and medial regions of prefrontal cortex support motivated behavior in large part by learning and representing value signals for expected and received rewards. An important mechanism potentially underlying the pursuit of rewards involves the contributions of midbrain dopaminergic neurons. Seminal rodent work indicates that lesioning projections of midbrain dopaminergic nuclei to the NAcc in rats inhibits cocaine self-administration (Robbins and others 1989; Robbins and Everitt 1996). Corroborating findings in humans come from fMRI studies of cocaine-addicted individuals, who demonstrate stronger responses in the NAcc during periods of drug craving (Breiter and others 1997). Furthermore, increased BOLD responses in the midbrain and dorsal striatum are observed in cocaine-addicted individuals during drug consumption (Breiter and others 1997). These results provide initial evidence that valued rewards, in this case drugs, can modulate activation in components of putative reward circuitry (e.g., ventral striatum) and that reward-related behaviors rely on this neural circuitry.

Stimulant drugs such as cocaine are extreme examples of reinforcers evoking reward value signals in the brain. Other types of primary reinforcers, such as food and juice, carry reward value because they satisfy basic survival needs (e.g., hunger, thirst), thus providing an impetus for motivated behavior. A host of human fMRI studies highlight the role of the striatum, medial PFC regions (particularly OFC) and midbrain (e.g., ventral tegmental area [VTA]) in representing reward value signals for primary reinforcers (Kringelbach and others 2003; O'Doherty and others 2002; O'Doherty and others 2003a). Neural responses in these regions support subjective ratings of stimulus value (e.g., pleasantness) (Kringelbach and others 2003; O'Doherty and others 2002), with functional dissociations demonstrated within the VTA (linearly tracks the subjective preference of outcome predicting cues) and the ventral striatum (preferentially responds to cues associated with the most and least preferred outcomes (O'Doherty and others 2006)). Patterns of activation reflecting more specific components of reward valuation processes have been reported in OFC. For example, blood oxygen level-dependent (BOLD) responses in medial and central OFC, respectively, reflect both the goal value (e.g., the expected value of a potential outcome) and the decision value (e.g., decision cost) when deciding which of varied primary reinforcers to pursue (Hare and others 2008; Plassmann and others 2007). Electrophysiological recordings in non-human primates corroborate a role for OFC in representing the value of primary reinforcers, showing that firing rates of OFC neurons track the reward value of a stimulus as well as changes in stimulus value over time (Clarke and others 2008; Ostlund and Balleine 2007). In summary, findings across species support the idea that primary reinforcers such as food are valued goals that can evoke reward value related activation in putative reward circuitry.

Survival in modern human society dictates that secondary reinforcers such as money—that is, a reinforcer that does not inherently satisfy basic biological drives—are also critical. A significant body of evidence indicates that valuation of monetary reinforcers is represented in the striatum and prefrontal cortex similarly to primary reinforcers (Bartra and others 2013). Anticipating impending monetary outcomes of varying valence (e.g., positive/gain, negative/loss) and magnitude (e.g., high, low) strongly recruits the ventral striatum (Knutson and others 2001) as well as the caudate nucleus (Bjork and others 2010); activation in these regions appears to scale linearly with the value of the monetary outcome. The striatum thus plays a role in tracking the subjective value of an expected reward (Hsu and others 2009; Knutson and others 2005). Adequately representing reward value also depends on some experience with the reward. When

winning (vs losing) money, the ventral striatum, caudate nucleus (Delgado and others 2000; Delgado and others 2003), the orbitofrontal cortex (Haruno and others 2004; O'Doherty and others 2001) and medial PFC (Knutson and others 2003) also demonstrate increased BOLD responses. These results not only highlight the fact that valuation of secondary reinforcers (e.g., monetary outcomes) rely on the striatum and medial prefrontal cortex, but further support the idea that reward value signals are encoded at different time-points (e.g., anticipation, experience), a point that will be revisited in the next section.

The value attributed to a reward depends on more than just its monetary value, or qualities as a food; rather, the context in which a reward is received can shape the subjective experience of that reward. Indeed, increased BOLD responses in the caudate nucleus are observed when a monetary reward is obtained in an active (vs. passive) manner (Elliott and others 2004; Tricomi and others 2006). This may result from the increased salience attributed to actively pursuing a reward (Zink and others 2004), or alternatively from a desire to link action and outcome (Tricomi and others 2004) when earning various types of rewards (Tricomi and Fiez 2008). Furthermore, striatal BOLD responses track outcome magnitude (Delgado and others 2003) and probability of outcome receipt (Delgado and others 2005b; Haruno and others 2004) as well the motivational salience of a secondary reinforcer (Delgado and others 2004). Taken together, this extensive literature indicates that the neural representation of expected and experienced reward value depends on the integration of multiple types of information.

Reward Learning

Neural signals representing expected and experienced reward value are vital because they can be integrated toward learning and adapting behavior. Associative and reinforcement learning theories (Niv 2009; Rescorla and Wagner 1972; Sutton and Barto 1998), suggest that learning is best when there is a mismatch between expectations and actual experience—i.e., a prediction error (Dayan and Niv 2008; Niv and Schoenbaum 2008). Midbrain dopaminergic nuclei and their targets appear to be integral for this type of learning process. Electrophysiological recordings from these nuclei in non-human primates support a role in trial-by-trial learning, with their activation patterns corresponding to a prediction-error signal (Bayer and Glimcher 2005; Niv and Schoenbaum 2008; Schultz and others 1997): peak firing rates are observed first to unexpected rewards, which shift over time (with learning) to the earliest predictor of the reward. Prediction-error learning is characterized by sensitivity to temporal aspects of delivery, as midbrain dopaminergic nuclei decrease firing when rewards are

not received at their expected time of delivery (Hollerman and Schultz 1998). A current outstanding debate within the literature is the precise nature of whether midbrain dopaminergic learning signals reflect only reward value or both reward and aversive value. Recent findings suggest that midbrain dopaminergic neurons code the presence of an unexpected reward, but not aversiveness or the absence of aversiveness, suggesting potential alternative neural mechanisms for representing other dimensions of value (Fiorillo 2013). A counterpoint to this argument however, is that differential midbrain dopaminergic neuronal populations are involved in representing reward and aversive components of value-based learning (Matsumoto and Hikosaka 2009). Suffice to say that midbrain dopaminergic neurons are critical for prediction-error based learning, but further research is needed to precisely define the nature of these signals (e.g., reward specific or not).

Inspired by the dopaminergic prediction-error hypothesis and findings from electrophysiological work reviewed above, neurocomputational approaches to studying reward-based learning in humans—for example, fitting reinforcement learning models to behavioral and fMRI data—consistently implicate the human striatum, particularly the ventral component. Prediction-error signals are observed in the ventral striatum during both Pavlovian and instrumental learning situations, suggesting a more general learning signal represented within this region (O'Doherty and others 2003a; O'Doherty and others 2004), which can be used to modify subsequent action–outcome based predictions (O'Doherty and others 2004). Action–outcome based predictions may rely on the dorsal striatum (O'Doherty and others 2004; Pennartz and others 2011), among other regions (Alexander and Brown 2011). A wealth of additional fMRI studies support a role for the ventral striatum as a component of a PE learning system (Daw and others 2011; Li and others 2011b; Schonberg and others 2007) that depends on dopaminergic modulation (Palminteri and others 2012; Pessiglione and others 2006). Related to the debate about the precise nature of learning signals being coded by mid-brain dopaminergic neurons, the role of the human striatum in prediction-error based learning is still being refined. Some recent evidence (Klein-Flügge and others 2011) indicates that the striatum may code task specific timing predictions, as opposed to a prediction-error learning signal per se. Another fMRI investigation reports positive prediction error responses in the VTA, the nature of which varies depending on the type of reinforcer used (e.g., primary/secondary), and both positive and negative prediction error signals in the ventral striatum for primary reinforcers only (D'Ardenne and others 2008). Still, additional evidence posits that computational signals within the ventral striatum reflect action-based updating (e.g., behavioral policy) as opposed to a value-based outcome

prediction error (Li and Daw 2011). Further work is needed to characterize the learning signals encoded within the striatum, but extant research reviewed above points to a significant role for this region in reward learning.

Learning to assign reward value via computational learning processes on a trial-by-trial basis clearly informs our understanding of the environment. A complementary process, however, involves keeping a record of the history of experienced outcomes and changing contingencies within the environment. Lesion studies and human fMRI studies point to mPFC regions, specifically parts of the anterior cingulate cortex (ACC), as a potential site for tracking such quantities. Lesioning the ACC sulcus in non-human primates impairs performance during a reward-based task requiring maintenance of action-outcome associations (Kennerley and others 2006). A similar area of the ACC in humans appears important for tracking outcome history during volatile conditions when learning about changing reward contingencies (Behrens and others 2007). A recent model (Alexander and Brown 2011) posits that mPFC and ACC specifically may serve to integrate reward-related information toward decision making. Alexander and Brown posit that the role of mPFC in reward valuation is to represent predictions regarding potential outcomes of chosen actions.

Learning based on expected and experienced outcomes is critical to successful adaptation to the environment. In conjunction with prefrontal cortical regions, the striatum serves to facilitate updating of outcome-based predictions. Though the focus of this review is on the striatum and medial PFC, it is important to note that other regions do contribute to prediction-based learning processes. For example, the amygdala and hippocampus are densely connected with the ventral striatum, as noted previously. One rodent model (Pennartz and others 2011) posits that the amygdala sends excitatory cue-based information to the ventral striatum, while the hippocampus contributes input regarding the context surrounding prediction-based learning. Thus, the ventral striatum may integrate a host of information toward outcome-based predictions. It is also worth noting that emerging fMRI evidence implicates other subcortical regions potentially playing a role in reward-learning, such as the hippocampus correlating with prediction error during probabilistic tasks (Dickerson and others 2011; Foerde and Shohamy 2011), and the amygdala, which has been linked to signaling a more general signal regarding associability of a stimulus with an outcome (Li and others 2011b).

Social Rewards

Human behavior frequently occurs within the context of social situations and interactions, versus in isolated

contexts as in the extant literature covering non-social reward processing described in the previous section. This is a crucial point to consider, because social information can influence our behaviors. As such, a complementary question is whether the valuation of social outcomes, or social rewards, relies on neural structures implicated in coding the value of primary and secondary non-social rewards, and how members of one's social network may further influence reward valuation processes.

Facial Attractiveness

Faces comprise one of the most extensive sets of social stimuli that we encounter as humans. Faces can be experienced or perceived across a variety of dimensions and provide a wealth of information about another person (e.g., trustworthiness) and the surrounding environment (e.g., impending threat). One such dimension that we can assess in looking at faces is attractiveness, which could be considered a metric of social reward value (Adolphs 2009; Adolphs and others 1998; Deaner and others 2005). An early foray into social reward processing highlighted that viewing attractive versus unattractive faces elicited stronger BOLD responses in mPFC and OFC (O'Doherty and others 2003b), and ventral striatum (Aharon and others 2001). More important, however, these regions parametrically tracked self-reported attractiveness ratings of facial stimuli suggesting that the subjective reward value of social stimuli—here, an attractive face—may be coded similarly to primary and secondary rewards (O'Doherty and others 2003b). If this idea is indeed correct, that attractiveness may be a social reward, then it should follow that attractiveness would serve to motivate behavior. Human males indeed wait longer and exert more effort to view a highly attractive (compared with a less attractive) female face (Aharon and others 2001; Hayden and others 2007) and BOLD responses in a posterior region of ventromedial PFC correlate with individuals' propensity to pay more money to view an attractive face (Smith and others 2010). Valuing social stimuli may well be a conserved process as rhesus macaques forgo juice rewards in order to view photos of socially desirable stimuli—for example, female perinea (Deaner and others 2005)—suggesting a possible evolutionary importance to social rewards.

Social Acceptance and Approval

Facial attractiveness may be a valued social signal because it can act as one of many social approach signals. In other words, beyond it being hedonically pleasant to view an attractive face, such stimuli could serve to motivate social approach behavior (e.g., starting a conversation), and generating expectations about whether we

would be accepted or rejected in our forays. An elegant study by Somerville and others (2006) highlights the role of the anterior cingulate in this process. They argued that the dorsal anterior cingulate cortex (dACC) distinguishes whether social expectations (e.g., will this person like me) are met or violated, with enhanced BOLD responses observed for violations. Ventral ACC (vACC), on the other hand, distinguishes between social outcome valence (e.g., accepted vs. rejected), showing stronger BOLD responses to positive social outcomes (e.g., being accepted) irrespective of expectation (Somerville and others 2006). Interestingly, this ventral ACC response is modulated by one's level of self-esteem—lower self-esteem is associated with stronger BOLD responses when accepted by others compared with individuals with higher self-esteem (Somerville and others 2010). Not only does being liked elicit BOLD activation in reward value-related circuitry (Davey and others 2010), but receiving positive character evaluations from another (e.g., being labeled trustworthy) elicits increases in striatal BOLD responses (Izuma and others 2008). This activation overlaps with striatal BOLD responses to those showing an increased response to a high amount of monetary reward in a non-social condition (Izuma and others 2008; see also Rademacher and others 2010). Together, these findings demonstrate that acceptance/approval may be treated as valued outcomes similarly to food or monetary rewards.

Moreover, while social acceptance or approval can be processed as a reward in and of itself, it can also motivate or change behavior. Participants demonstrate an increased tendency to make charitable donations to certain organizations when being observed with a potential to receive approval for their behavior compared to when making the same decision in isolation (Fehr and Camerer 2007; Izuma and others 2010; Rilling and Sanfey 2011). Furthermore, ventral striatal BOLD responses show increased BOLD activity when participants decided to donate with the chance for approval, compared to when making the same decision alone (Izuma and others 2010). While the ventral striatum has been implicated in prosocial decisions such as charitable giving (Harbaugh and others 2007), the opportunity for social approval appears to bring an added motivating factor during decision making. It is possible that these social outcomes provide some way of satisfying one's need to belong, and may be a first step toward establishing a social relationship.

Social Decision Making

Navigating our social world requires more than just generating expectations as to whether we will be liked by others and judging facial attractiveness. While social signals such as attractiveness and acceptance can carry

reward value, we must engage in repeated interactions in order to truly become accepted by others and build relationships (King-Casas and others 2005; van Winden and others 2008).

Social interactions involve a concern for social preferences such as fairness and cooperation (Fehr and Camerer 2007; Rilling and Sanfey 2011). These preferences allow us not only to evaluate others but also allow for them to evaluate us on more than just appearance. Humans often reject inequity or perceived unfairness in bargaining situations (Güth and others 1982) and act against their material self-interest toward a common goal perhaps out of a concern for reputation and expectation of reciprocity (Berg and others 1995). Cooperation in particular during interactions allows us to learn about others and can facilitate building of relationships. It has been suggested that cooperation may be evolutionarily adaptive in part because it may lead to future success (Axelrod and Hamilton 1981), and as many interactions are repeated (e.g., with the same people), decisions to cooperate may be intuitive or a “default” mode of response (Rand and others 2012).

Put another way, cooperation may be a form of social reward because it confers social benefits. Cooperation is typically measured using a paradigm known as the Prisoner's Dilemma Game (Rapoport and Chammah 1965) in which two parties simultaneously decide whether to cooperate with each other to achieve a mutually beneficial outcome or to defect in hopes of achieving maximal personal gain. Participants generally choose to cooperate with human partners toward mutually beneficial outcomes, and the ventral striatum, mPFC, and ACC are involved in processing outcomes achieved through mutual cooperation (Rilling and others 2002; Rilling and others 2004). These findings support the notion that cooperation can act as a valued social signal or reward.

One construct underlying cooperative behavior is trust. Within the context of decision making within social interactions, trust may be conceived of as involving expectations of reciprocity; that is, the extent to which we believe another person will exhibit reciprocal behavior (Cox 2004). Learning about another can thus occur by forming an expectation about him/her when deciding whether to pursue an interaction, and then observing whether the interaction's outcome matches our expectation. This is akin to trial-by-trial based learning processes observed in non-social situations (Niv and Schoenbaum 2008; Schultz and others 1997), and recent evidence suggests that social learning processes may rely on similar neurocomputational (e.g., prediction error) mechanisms (Kishida and Montague 2012).

A two-party exchange game known as the trust game (Berg and others 1995) has proven useful in examining trust behavior in social interactions. Here, one person

(designated the investor) decides whether to keep all of a given sum of money or send some percentage of it to a second party (designated the trustee). Choices to send money result in that amount of sent money being multiplied by a factor of three or four, of which the trustee can then decide on an amount to return, if desired. fMRI investigations of social learning via the trust game implicate reward-based mechanisms in learning a partner's reputation for reciprocity. BOLD responses in the caudate nucleus of trustees in a repeated trust game paradigm show a prediction error-like response that shifts in time to the earliest predictor of an investor's generosity (King-Casas and others 2005). Thus, interactions based on trust suggest that trust is akin to a social expectation which relies on a prediction-error based learning signal. In fact, learning about a partner may depend on dopaminergic influence (Eisenegger and others 2013). The root of trust-based interactions is reciprocity, and this may function as a valued social reward in and of itself: participants demonstrate a propensity to trust more cooperative partners (e.g., those exhibiting reciprocity), and BOLD responses in the ventral striatum are observed as strongest when cooperative (vs. uncooperative) partners reciprocate trust (Phan and others 2010).

Appraisals of partners as trustworthy and decisions to trust depend on more than patterns of reciprocity. Some evidence suggests that trustworthiness is a dynamically evolving belief, drawing not only on a partner's patterns of reciprocity but also taking into account social signals appraised from facial characteristics (Chang and others 2010). Furthermore, our behavior in trust-based social interactions can be colored by prior beliefs or impressions of others we may bring to a subsequent interaction (Delgado and others 2005a). Impressions of others may be obtained even before interacting with them (e.g., reading or being told information about a person's moral character—instructed means). Such prior impressions (see Fig. 2) can shape how we respond to actual outcomes of interactions with a partner such that we tend to act in accordance with prior impressions in the face of competing information. For example, we may be more likely to trust someone of whom we have a positive impression, regardless of whether they continue to act in a trustworthy manner (Delgado and others 2005a; see Figs. 2A and 3B). Furthermore, impressions gained from prior social experience (Fareri and others 2012a; see Figs. 2B and 3C) in different contexts (e.g., not a trust-based interaction) tend to bias learning mechanisms to rely on information consistent with initial impressions when subsequently updating reputations about partners.

Outside influences on reputation learning may be a result of the interaction of multiple learning and memory systems. Indeed, emerging evidence suggests that multiple systems in the brain likely interact with each other to

contribute to decision making (Delgado and Dickerson 2012; Packard and Knowlton 2002; Shohamy 2011; Shohamy and Adcock 2010). Within social interactions, learning information about an interaction partner through instructed or declarative means (Delgado and others 2005a; see Fig. 2A) may be encoded via prefrontal and/or hippocampal systems supporting declarative or episodic learning (Doll and others 2009). These systems may subsequently modulate the ability of striatal-based experiential learning systems to incorporate new social information (e.g., interaction outcomes) on a trial-by-trial basis (Delgado and others 2005a; see Fig. 3B). This top-down modulation of social learning would be consistent with evidence from non-social situations demonstrating blunted striatal learning signals after instructed information regarding task contingencies (Li and others 2011a). Learning initial social information via experience in different contexts (e.g., forming an impression of someone at work and then encountering them in a personal setting), conversely, may bias behavior and learning by amplifying trial-by-trial sensitivity to consistent social information (Fareri and others 2012a; see Figs. 2B and 3C).

Social Network and Reward

The idea of using past experience or knowledge about another person to guide behavior, particularly when consistent, is interesting within the context of establishing a relationship. Reciprocity of trusting behavior is a valued social signal which informs learning of reputation and, in addition to other considerations (van Winden and others 2008), supports building a close relationship. Indeed, a social need for belongingness entails a desire to have consistent interactions with another person that are stable, empathic and long-term, and associated with positive affect (Baumeister and Leary 1995). Once a relationship is established with another person who presumably becomes part of our social network, we typically seek out continued interactions characterized by positive experiences involving self-disclosure, emotional support and trust (Fehr 2004; van Winden and others 2008). Furthermore, close, in-network relationships involve merged representations of self and other such that a close other's characteristics and resources are often perceived as one's own, facilitating social closeness (Aron and others 1991). It is possible that continued positive interactions within established relationships serve to solidify or reaffirm bonds or relationships. These factors—closeness, support, trust—which typify close, in-network relationships, may bring about positive affect and reinforcing effects, a potential underlying mechanism for continued pursuit of in-network interactions (Baumeister and Leary 1995).

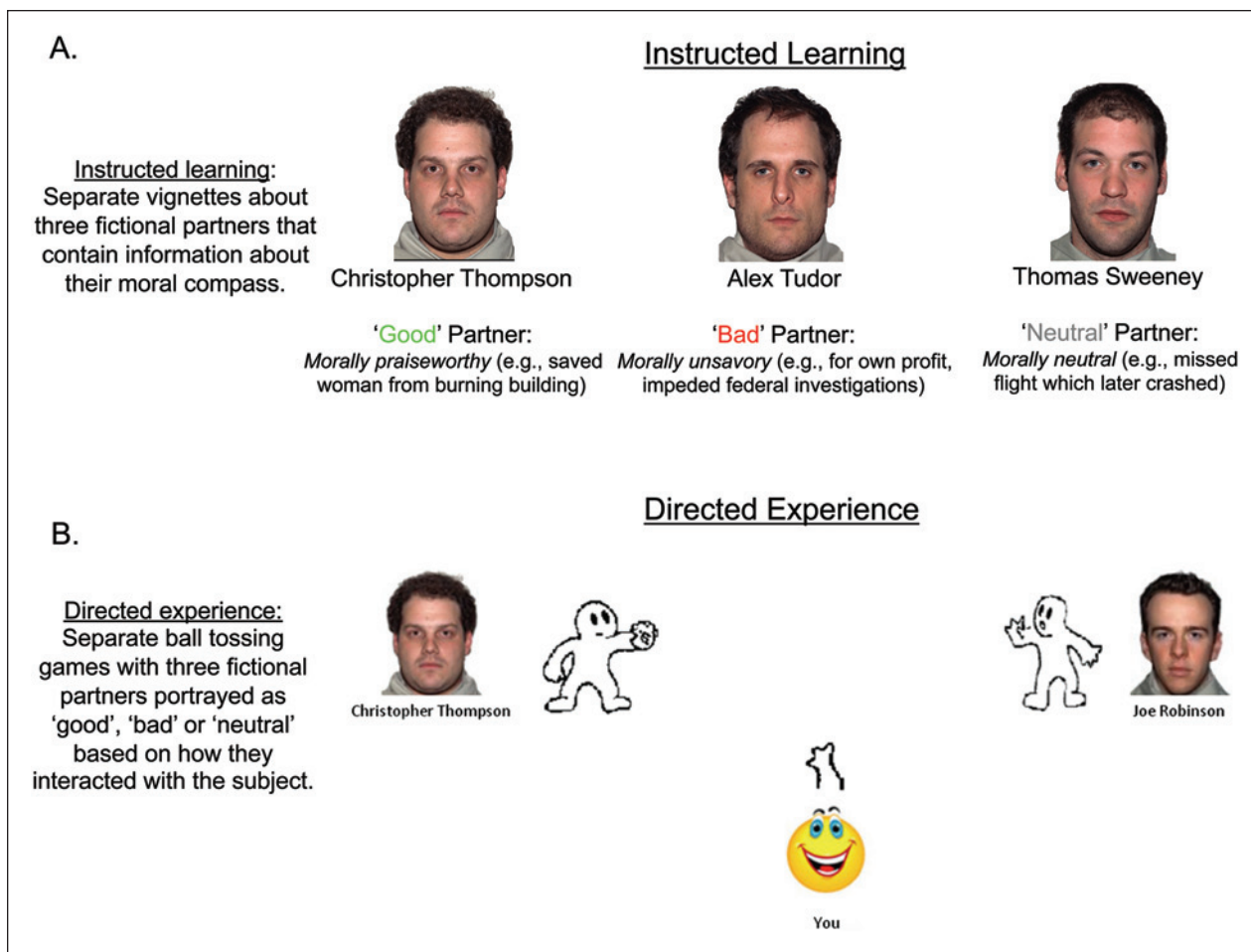


Figure 2. Task designs for investigating effects of prior social information acquired through instructed means or through direct social experience on responses to trust interactions. (A) Instructed learning manipulation employed by Delgado and others (2005a). Participants were presented with three vignettes about three fictional partners with whom they were to subsequently interact in an iterated economic trust game. Personalities of the partners were manipulated within the vignettes to provide information regarding their moral character and depict them as being morally praiseworthy (i.e., good), morally unsavory (i.e., bad), or morally neutral. This manipulation was intended to influence participants' decisions to trust each partner in the subsequent trust game. No information regarding the neutral partner's moral disposition was provided; the vignette for this partner was constructed to be similarly arousing to the others, while lacking any direct involvement or action of the partner on the surrounding events. All participants experienced all three conditions. (B) Direct social experience manipulation employed by Fareri and others (2012a). Participants interacted with fictional partners via a computerized ball-tossing game (Williams and others 2000) with whom they would later play an iterated economic trust game. Participants played three different versions of the ball tossing game, each with one partner whose personality was manipulated with respect to the manner in which they interacted with participants (e.g., always throw to participant, never throw to participant, throw to the participant half of the time). Each version of the game also included a control partner whose personality was consistently neutral across all versions of the game, and who was not included in the subsequent trust game.

Exciting recent evidence has begun to broach the relationship between social networks/close relationships and neural structure and function. An interesting and influential hypothesis supporting the importance of investigating this link is that our brain may have evolved in conjunction with, or to support, increased sociality and formation of social groups (Adolphs 2009). Accordingly, positive correlations are reported between

amygdala volume and both the size (e.g., number of members) and complexity (how many subgroups members of one's social network belong to) of participants' real-world (Bickart and others 2011) and online (Kani and others 2012) social networks. Moreover, social network size and the strength of intrinsic (resting state) functional connectivity between medial amygdala nuclei and areas involved in affiliative behaviors

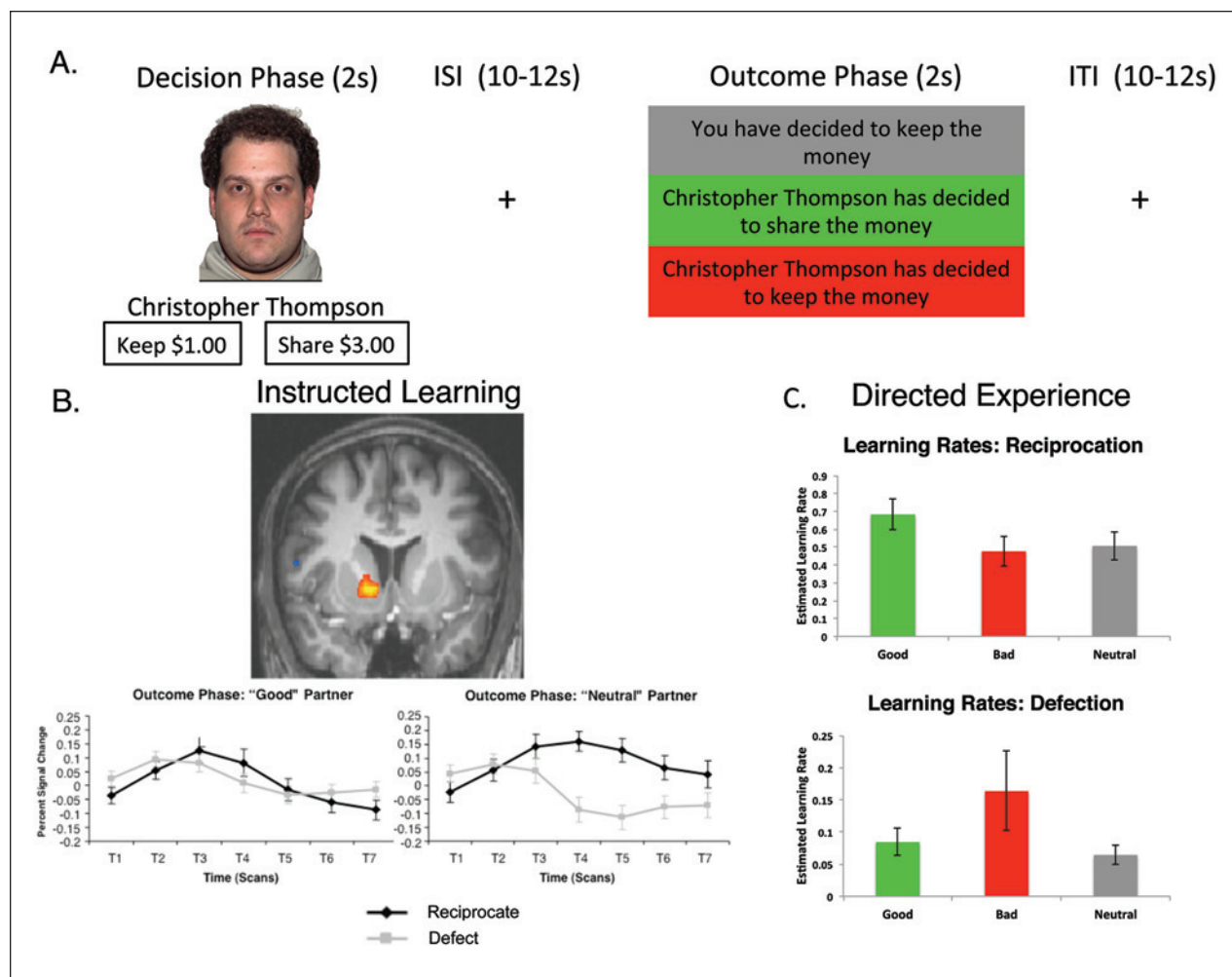


Figure 3. Trust game task design and results from Delgado and others (2005a) and Fareri and others (2012a). (A) In the trust game, participants played as investors, endowed with \$1.00 on each trial. Participants repeatedly interacted with one of the three partners about whom they had previously learned on each trial and were presented with a photo of the partner and a choice between two decision options. Participants could choose to keep the \$1.00 for themselves or share/invest it with their partner. A choice to share resulted in a multiplied amount of money (\$3.00) going to the partner, whereas a choice to keep ended the trial. If participants chose to share, their partner could then either return half of the shared amount (\$1.50) to the participant (reciprocate) or keep all \$3.00, leaving the participant with nothing on that trial (defect). (B) When initially learning social information about a partner through instructed means (Delgado and others, 2005a), neural responses in the striatum to partner choices in the trust game are modulated by prior impressions. A differential response in the striatum to partner choice (reciprocate or defect) was observed when no strong prior information about that partner was available (neutral partner); however, when strong prior information was available (good partner), the striatum did not differentiate trust game outcomes, suggesting social modulation of striatal responses. Figure adapted from Delgado and others (2005a), *Nature Neuroscience* (8)11:1611-1618. (C) When initially learning social information via directed experience in a different context (Fareri and others 2012a), participants rely behaviorally on information consistent with initial social information to update their beliefs about their partners in the trust game. That is, participants are more likely to rely on reciprocation to update beliefs about their partners when they have a positive prior impression of said partner, and more likely to rely on defection for partners carrying a negative prior impression. Figure adapted from Fareri and others (2012a), *Frontiers in Decision Neuroscience* (6)148. doi: 10.3389/fnins.2012.00148

(subgenual ACC, ventral striatum) also demonstrate a strong relationship (Bickart and others 2012). These results suggest an important link between social network and neural organization.

The relationship between social network and neural function is equally interesting, yet even less characterized. Initial evidence laying the groundwork for investigating this interaction point to involvement of reward

valuation regions in experiences with “similar” others and vicarious reinforcement (Mobbs and others 2009). Mobbs and colleagues revealed that BOLD responses in the ventral striatum are similar both when achieving monetary rewards in a game and when viewing a socially desirable other have success in the same game. Furthermore, they demonstrated that the strength of connectivity between ventral striatum and vACC when viewing a socially desirable other have success positively correlated with how similar to oneself this person was perceived. Perceptions of others as similar and/or desirable may therefore influence processing of reward value. This is of note given that similar evidence has emerged in non-human primates. Rhesus macaques prefer cues predictive of a reward going to a conspecific over those which predict reward to neither the self nor other (Chang and others 2011). Notably, the ACC gyrus appears to signal reward administration to self, other and both (Chang and others 2012), suggesting related neural processes in coding social and vicarious reward across species.

The findings reviewed in this section lay important groundwork for investigating relationships between social network and neural function. One recent study (Meshi and others 2013) reports that BOLD responses in the ventral striatum to positive social feedback—for example, character evaluations (Izuma and others 2008)—is linearly related to the degree to which a person uses and is invested in Facebook. Interestingly, ventral striatal response to monetary reward receipt is not related to Facebook usage, suggesting something unique about the social reward of a positive evaluation. Another prism through which to think about the effects of social network on day-to-day behavior and neural function is to consider how the social context created by members of our social networks influences the value placed on social experiences (Fareri and others 2012b; Fareri and Delgado 2013; see Figs. 4 and 5). For example, one common social experience is that of pursuing a shared reward with another (e.g., working on a class project, trying to win a competition together). If our social existence is driven by a need to have continued positive interactions with another person, then shared experiences with an in-network other (e.g., someone with whom there is a close relationship) may carry increased value compared shared positive experiences with someone with whom we share a more distant relationship. Indeed, emerging evidence (see Fig. 4) indicates that shared positive (monetary) outcomes with an in-network other (close friend) carry increased value as compared to monetary gains shared with an out-of-network other (confederate) or a non-social entity (computer), as reflected in subjective ratings and enhanced ventral striatal BOLD responses (Fareri and others 2012b). Importantly, this pattern of BOLD responses was related to how close participants were to

their friend (e.g., closer participants exhibited this distinction more so than those who were less close), suggesting closeness as a potential mechanism for the increased value of a shared in-network reward. This finding is in line with models implicating relationship closeness and attachment as important for social reward processing (Vrtička and Vuilleumier 2012), as well as those suggesting that continued positive interaction and experiences may reaffirm a close relationship (Baumeister and Leary 1995). Indeed, within close relationships, evidence points to an enhanced propensity to pursue continued interactions with in-network (vs. out-of-network others) others with ventral striatal BOLD signals to reciprocation of trust from an in-network other stronger than reciprocation from an out-of-network other or non-social entity (Fareri and others 2013).

Discussion

Establishing social relationships and being part of social networks are crucial to human survival, providing a means to meet social needs. Socially relevant rewards—for example, attractiveness, approval, acceptance, reciprocity—can all serve as valued social rewards in and of themselves, and rely on neural mechanisms (e.g., corticostriatal reward circuitry) that support reward valuation in non-social contexts. More important, social rewards can provide gateways toward learning about others, building personal social networks, and establishing close relationships (e.g., close friendships, romantic relationships). Repeated (positive) experiences with close in-network others may be of significant value because they reaffirm a need to belong and continually solidify social bonds. Recent evidence suggests that positive experiences with close in-network others are unique and processed differently than similar experiences with those less close or even unknown (Fareri and others 2012b). However, given the increased importance of social network and social connection not only in modern society, but in terms of an evolutionary context, more efforts are needed to characterize the interaction of social rewards and social network on brain and behavior.

Evidence characterizing the value of social rewards (e.g., attractive faces), highlight the fact that extra effort is made to pursue more highly valued social stimuli across species (Deaner and others 2005; Hayden and others 2007), which is borne out by corroborating neural signals in putative reward circuitry (Smith and others 2010). Future investigations may attempt to more computationally define the value of an in-network relationship (e.g., how much one would be willing to pay or sacrifice to interact with an in- vs. out-of-network other). Furthermore, multiple models suggest an interaction between reward-based mechanisms and social attachment/affiliative

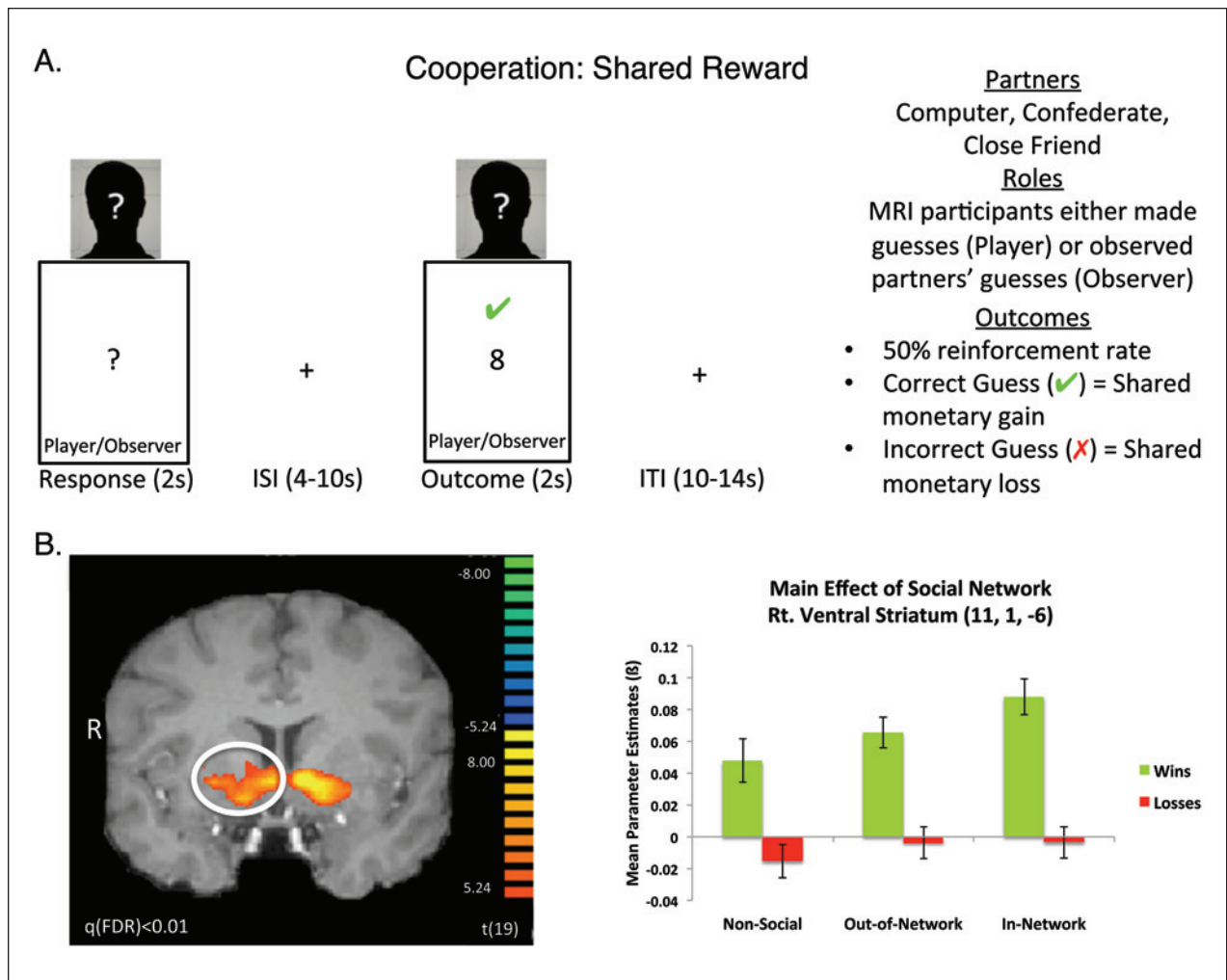


Figure 4. Effects of social network on neural outcome value signals coding shared rewards. (A) During a shared social context, participants played a computerized card-guessing task with a non-social (computer), out-of-network (confederate), and in-network (close friend) partner for shared monetary outcomes (Fareri and others 2012b). A simple card-guessing task was administered, the goal of which was to make a binary guess as to whether the numerical value of card was higher or lower than the number 5. A correct guess resulted in the presentation of the value of the card and a green check mark indicating a monetary gain of \$4.00; an incorrect guess resulted in the presentation of the numerical value of the card and a red “X” above it, indicating a monetary loss of \$2.00. Participants took turns making guesses (Player role) or watching their partners make guesses (Observer role) and played with one partner on each trial of the task as indicated by a photo at the top of the screen. Participants and their partners were told that all outcomes were shared between whoever was playing on a given trial. Thus, a correct guess on a given trial would result in a gain of \$4.00 being split evenly between the MRI participant and their partner (+\$2.00 each), and an incorrect guess would result in a monetary loss of \$2.00 being split evenly between the MRI participant and their partner (−\$1.00 each). In reality, an equal amount of monetary gains and losses were administered to ensure an equivalent experience across participants. (B) The ventral striatum differentiates shared monetary gains (wins), but not losses, as a function of social network, with strongest responses when sharing monetary gain with a close friend. This pattern of activation suggesting increased value to sharing a positive experience with an in-network other. Figure adapted from Fareri and others (2012b), *The Journal of Neuroscience* (32)26:9045-52.

mechanisms in the formation of close social relationships (Bickart and others 2012; Vrtička and Vuilleumier 2012). An interesting outstanding question in the literature is not only how neural systems interact to support processing of social reward and in- versus out-of-network experiences,

but also how hormones involved in affiliative behaviors and relationship formation (Insel and Young 2001; Vrtička and Vuilleumier 2012) and genetic factors may come into play as potential modulating factors in the sensitivity to the value of in-network relationships.

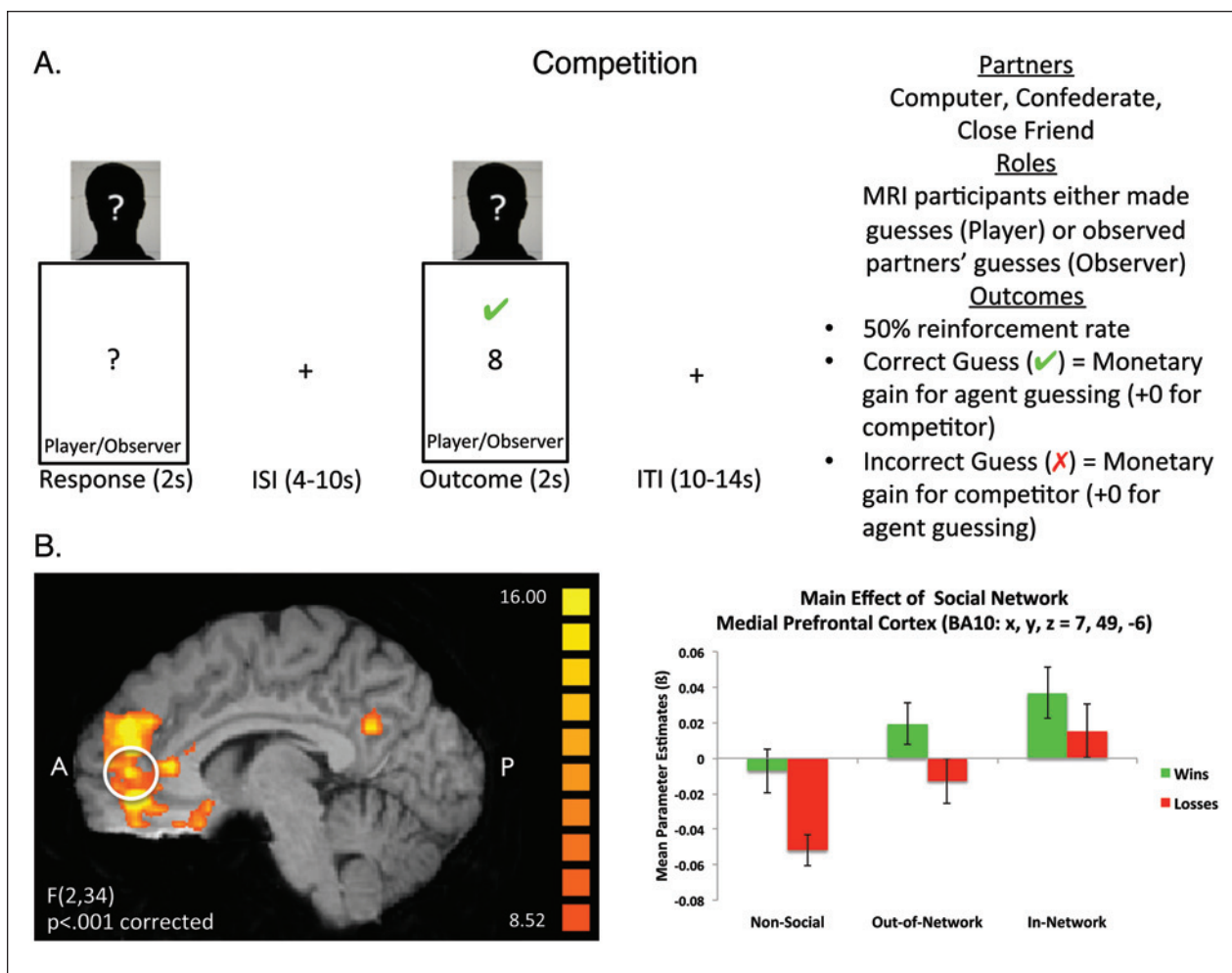


Figure 5. Effects of social network on neural outcome value signals during a competitive social context. (A) During a competitive social context (Fareri and Delgado 2013), participants competed for monetary outcomes with a non-social (computer), out-of-network (confederate), and in-network (close friend). A simple card-guessing task was administered as described in Figure 4, but with an important modification to how outcomes were administered. As this was a competitive context, a correct guess in the task resulted in a monetary gain (+\$2.00) for whichever agent was guessing on a given trial (e.g., MRI participant or one of the three competitors), and no gain (+\$0.00) for the other agent. An incorrect guess resulted in no monetary gain (+\$2.00) for the agent guessing and a monetary gain (+\$2.00) for the other agent. (B) Robust responses in medial prefrontal cortex emerge during outcome processing. When collapsing across valence, medial prefrontal cortex exhibits enhanced blood oxygen level–dependent (BOLD) responses when competing against an in-network other, suggesting an enhanced value to outcomes experienced against an in-network competitor. Figure adapted from Fareri and Delgado (2013), *Social, Cognitive, Affective Neuroscience*, doi:10.1093/scan/nst006.

Social networks and close relationships are important throughout life, but perhaps at no more critical time than during development. Adolescence in particular is a time during which social networks characterized by peers begin to take on increasing importance (Steinberg 2008). It is possible that approval and social outcomes administered by peers become more highly valued (Costanzo and Shaw 1966) than approval from, for example, parents or other authority figures. Developmental investigations have begun to probe decision making within social contexts. For example, adolescents tend to make increased

risky-driving decisions (e.g., running a yellow light as opposed to slowing down) when being observed by peers compared with older individuals (Chein and others 2011; Gardner and Steinberg 2005); this behavioral tendency is associated with increased ventral striatal BOLD responses and decreased prefrontal BOLD responses when making these decisions in the context of peers, compared with when in a non-social context (Chein and others 2011). These findings suggest the importance of investigating the influence of social context on reward-related decision-making within developmental samples. However, future

work could be aimed at characterizing the neural and behavioral developmental time-course pertaining to the value of in-network interactions and positive experiences with in-network versus out-of-network others. Findings from such investigations have the ability to elucidate mechanisms by which social network and close relationships may influence decision-making during development, over and above a more general social influence.

Acknowledgments

The authors would like to acknowledge Anastasia Rigney for helpful comments.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: This work was supported by funding from the National Institute of Mental Health (NIMH) to MRD, titled "Modulation of Human Reward Circuitry by Social Factors" (Grant No. R01MH084081).

References

- Adolphs R, Tranel D, Damasio A. 1998. The human amygdala in social judgment. *Nature* 393:470–4.
- Adolphs R. 2009. The social brain: neural basis of social knowledge. *Annu Rev Psychol* 60:693–716.
- Aharon I, Etcoff N, Ariely D, Chabris CF, O'Connor E, Breiter HC. 2001. Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron* 32:537–51.
- Alexander GE, DeLong MR, Strick PL. 1986. Parallel organization of functionally segregated circuits linking basal ganglia and cortex. *Annu Rev Neurosci* 9:357–81.
- Alexander WH, Brown JW. 2011. Medial prefrontal cortex as an action-outcome predictor. *Nat Neurosci* 14:1338–44.
- Aron A, Aron EN, Tudor M, Nelson G. 1991. Close relationships as including other in the self. *J Pers Soc Psychol* 60:241–53.
- Axelrod R, Hamilton W. 1981. The evolution of cooperation. *Science* 211:1390–6.
- Bartra O, McGuire JT, Kable JW. 2013. The valuation system: a coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. *Neuroimage* 76:412–27.
- Baumeister R, Leary M. 1995. The need to belong: desire for interpersonal attachments as a fundamental human motivation. *Psychol Bull* 117:497–529.
- Bayer HM, Glimcher PW. 2005. Midbrain dopamine neurons encode a quantitative reward prediction error signal. *Neuron* 47:129–41.
- Behrens TE, Woolrich MW, Walton ME, Rushworth MF. 2007. Learning the value of information in an uncertain world. *Nat Neurosci* 10:1214–21.
- Berg J, Dickhaut J, McCabe K. 1995. Trust, reciprocity, and social history. *Games Econ Behav* 10:122–42.
- Bhanji JP, Delgado MR. 2014. The social brain and reward: social information processing in the human striatum. *Wiley Interdiscip Rev Cogn Sci* 5:61–73.
- Bickart KC, Hollenbeck MC, Barrett LF, Dickerson BC. 2012. Intrinsic amygdala-cortical functional connectivity predicts social network size in humans. *J Neurosci* 32:14729–41.
- Bickart KC, Wright CI, Dautoff RJ, Dickerson BC, Barrett LF. 2011. Amygdala volume and social network size in humans. *Nat Neurosci* 14:163–4.
- Bjork JM, Smith AR, Chen G, Hommer DW. 2010. Adolescents, adults and rewards: comparing motivational neurocircuitry recruitment using fMRI. *PLoS One* 5:e11440.
- Breiter HC, Gollub RL, Weisskoff RM, Kennedy DN, Makris N, Berke JD, and others. 1997. Acute effects of cocaine on human brain activity and emotion. *Neuron* 19:591–611.
- Chang LJ, Doll BB, van't Wout M, Frank MJ, Sanfey AG. 2010. Seeing is believing: trustworthiness as a dynamic belief. *Cogn Psychol* 61:87–105.
- Chang SW, Gariépy J-F, Platt ML. 2012. Neuronal reference frames for social decisions in primate frontal cortex. *Nat Neurosci* 16:243–50.
- Chang SW, Winecoff AA, Platt ML. 2011. Vicarious reinforcement in rhesus macaques (*Macaca mulatta*). *Front Neurosci* 5:27.
- Chein J, Albert D, O'Brien L, Uckert K, Steinberg L. 2011. Peers increase adolescent risk taking by enhancing activity in the brain's reward circuitry. *Dev Sci* 14:F1–10.
- Clarke HF, Robbins TW, Roberts AC. 2008. Lesions of the medial striatum in monkeys produce perseverative impairments during reversal learning similar to those produced by lesions of the orbitofrontal cortex. *J Neurosci* 28:10972–82.
- Costanzo PR, Shaw ME. 1966. Conformity as a function of age level. *Child Dev* 37:1531–43.
- Cox J. 2004. How to identify trust and reciprocity. *Games Econ Behav* 46:260–81.
- D'Ardenne K, McClure SM, Nystrom LE, Cohen JD. 2008. BOLD responses reflecting dopaminergic signals in the human ventral tegmental area. *Science* 319:1264–7.
- Davey CG, Allen NB, Harrison BJ, Dwyer DB, Yücel M. 2010. Being liked activates primary reward and midline self-related brain regions. *Hum Brain Mapp* 31:660–8.
- Daw ND, Gershman SJ, Seymour B, Dayan P, Dolan RJ. 2011. Model-based influences on humans' choices and striatal prediction errors. *Neuron* 69:1204–15.
- Dayan P, Niv Y. 2008. Reinforcement learning: the good, the bad and the ugly. *Curr Opin Neurobiol* 18:185–96.
- Deaner RO, Khera AV, Platt ML. 2005. Monkeys pay per view: adaptive valuation of social images by rhesus macaques. *Curr Biol* 15:543–8.
- Delgado MR. 2007. Reward-related responses in the human striatum. *Ann N Y Acad Sci* 1104:70–88.
- Delgado MR, Dickerson KC. 2012. Reward-related learning via multiple memory systems. *Biol Psychiatry* 72:134–41.
- Delgado MR, Frank R, Phelps EA. 2005a. Perceptions of moral character modulate the neural systems of reward during the trust game. *Nat Neurosci* 8:1611–8.

- Delgado MR, Locke H, Stenger VA, Fiez JA. 2003. Dorsal striatum responses to reward and punishment: effects of valence and magnitude manipulations. *Cogn Affect Behav Neurosci* 3:27–38.
- Delgado MR, Miller M, Inati S, Phelps EA. 2005b. An fMRI study of reward-related probability learning. *Neuroimage* 24:862–73.
- Delgado MR, Nystrom LE, Fissell C, Noll D, Fiez JA. 2000. Tracking the hemodynamic responses to reward and punishment in the striatum. *J Neurophysiol* 84:3072–7.
- Delgado MR, Stenger VA, Fiez JA. 2004. Motivation-dependent responses in the human caudate nucleus. *Cereb Cortex* 14:1022–30.
- Dickerson KC, Li J, Delgado MR. 2011. Parallel contributions of distinct human memory systems during probabilistic learning. *Neuroimage* 55:266–76.
- Doll BB, Jacobs WJ, Sanfey AG, Frank MJ. 2009. Instructional control of reinforcement learning: a behavioral and neuro-computational investigation. *Brain Res* 1299:74–94.
- Dunbar RI. 2012. Bridging the bonding gap: the transition from primates to humans. *Philos Trans R Soc Lond B Biol Sci* 367:1837–46.
- Eisenegger C, Pedroni A, Rieskamp J, Zehnder C, Ebstein R, Fehr E, and others. 2013. DAT1 polymorphism determines L-DOPA effects on learning about others' prosociality. *PLoS One* 8:e67820.
- Elliott R, Newman JL, Longe OA, William Deakin JF. 2004. Instrumental responding for rewards is associated with enhanced neuronal response in subcortical reward systems. *Neuroimage* 21:984–90.
- Fareri DS, Chang LJ, Delgado MR. 2012a. Effects of direct social experience on trust decisions and neural reward circuitry. *Front Dec Neurosci* 6:148.
- Fareri DS, Chang LJ, Delgado MR. 2013. How real-life prior experience influences trust decisions and reward learning mechanisms. Paper presented at: 20th Annual Meeting of the Cognitive Neuroscience Society, San Francisco, CA.
- Fareri DS, Delgado MR. 2013. Differential reward responses during competition against in and out-of-network others. *Soc Cogn Affect Neurosci*. Epub Jan 22.
- Fareri DS, Niznikiewicz MA, Lee VK, Delgado MR. 2012b. Social network modulation of reward-related signals. *J Neurosci* 32:9045–52.
- Fehr B. 2004. Intimacy expectations in same-sex friendships: a prototype interaction-pattern model. *J Pers Soc Psychol* 86:265–84.
- Fehr E, Camerer CF. 2007. Social neuroeconomics: the neural circuitry of social preferences. *Trends Cogn Sci* 11:419–27.
- Fiorillo CD. 2013. Two dimensions of value: dopamine neurons represent reward but not aversiveness. *Science* 341:546–9.
- Foerde K, Shohamy D. 2011. Feedback timing modulates brain systems for learning in humans. *J Neurosci* 31:13157–67.
- Gardner M, Steinberg L. 2005. Peer influence on risk taking, risk preference, and risky decision making in adolescence and adulthood: an experimental study. *Dev Psychol* 41:625–35.
- Groenewegen H, Wright C, Beijer A, Voorn P. 1999. Convergence and segregation of ventral striatal inputs and outputs. *Ann N Y Acad Sci* 877:49–63.
- Güth W, Schmittberger R, Schwarze B. 1982. An experimental analysis of ultimatum bargaining. *J Econ Behav Organ* 3:367–88.
- Haber SN, Fudge JL, McFarland NR. 2000. Striatonigrostriatal pathways in primates form an ascending spiral from the shell to the dorsolateral striatum. *Neuroimage* 20:2369–82.
- Haber SN, Knutson B. 2010. The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacology* 35:4–26.
- Harbaugh WT, Mayr U, Burghart DR. 2007. Neural responses to taxation and voluntary giving reveal motives for charitable donations. *Science* 316:1622–5.
- Hare TA, O'Doherty J, Camerer CF, Schultz W, Rangel A. 2008. Dissociating the role of the orbitofrontal cortex and the striatum in the computation of goal values and prediction errors. *J Neurosci* 28:5623–30.
- Haruno M, Kuroda T, Doya K, Toyama K, Kimura M, Samejima K, and others. 2004. A neural correlate of reward-based behavioral learning in caudate nucleus: a functional magnetic resonance imaging study of a stochastic decision task. *J Neurosci* 24:1660–5.
- Hayden BY, Parikh PC, Deane RO, Platt ML. 2007. Economic principles motivating social attention in humans. *Proc Biol Sci* 274:1751–6.
- Hollerman J, Schultz W. 1998. Dopamine neurons report an error in the temporal prediction of reward during learning. *Nat Neurosci* 1:304–9.
- Hsu M, Krajbich I, Zhao C, Camerer CF. 2009. Neural response to reward anticipation under risk is nonlinear in probabilities. *J Neurosci* 29:2231–7.
- Insel TR, Young LJ. 2001. The neurobiology of attachment. *Nat Rev Neurosci* 2:129–36.
- Izuma K, Saito DN, Sadato N. 2008. Processing of social and monetary rewards in the human striatum. *Neuron* 58:284–94.
- Izuma K, Saito DN, Sadato N. 2010. Processing of the incentive for social approval in the ventral striatum during charitable donation. *J Cogn Neurosci* 22:621–31.
- Kanai R, Bahrami B, Roylance R, Rees G. 2012. Online social network size is reflected in human brain structure. *Proc Biol Sci* 279:1327–34.
- Kennerley SW, Walton ME, Behrens TE, Buckley MJ, Rushworth MF. 2006. Optimal decision making and the anterior cingulate cortex. *Nat Neurosci* 9:940–7.
- King-Casas B, Tomlin D, Anen C, Camerer C, Quartz S, Montague P. 2005. Getting to know you: reputation and trust in a two-person economic exchange. *Science* 308:78–83.
- Kishida KT, Montague PR. 2012. Imaging models of valuation during social interaction in humans. *Biol Psychiatry* 72:93–100.
- Klein-Flügge MC, Hunt LT, Bach DR, Dolan RJ, Behrens TE. 2011. Dissociable reward and timing signals in human mid-brain and ventral striatum. *Neuron* 72:654–64.
- Knutson B, Adams C, Fong G, Hommer D. 2001. Anticipation of increasing monetary reward selectively recruits nucleus accumbens. *J Neurosci* 21:RC159.
- Knutson B, Fong GW, Bennett SM, Adams CM, Hommer D. 2003. A region of mesial prefrontal cortex tracks monetarily

- rewarding outcomes: characterization with rapid event-related fMRI. *Neuroimage* 18:263–72.
- Knutson B, Taylor J, Kaufman M, Peterson R, Glover G. 2005. Distributed neural representation of expected value. *J Neurosci* 25:4806–12.
- Kringelbach ML, O'Doherty J, Rolls ET, Andrews C. 2003. Activation of the human orbitofrontal cortex to a liquid food stimulus is correlated with its subjective pleasantness. *Cereb Cortex* 13:1064–71.
- Li J, Daw ND. 2011. Signals in human striatum are appropriate for policy update rather than value prediction. *J Neurosci* 31:5504–11.
- Li J, Delgado MR, Phelps EA. 2011a. How instructed knowledge modulates the neural systems of reward learning. *Proc Natl Acad Sci U S A* 108:55–60.
- Li J, Schiller D, Schoenbaum G, Phelps EA, Daw ND. 2011b. Differential roles of human striatum and amygdala in associative learning. *Nat Neurosci* 14:1250–1252.
- Matsumoto M, Hikosaka O. 2009. Two types of dopamine neuron distinctly convey positive and negative motivational signals. *Nature* 459:837–41.
- Meshi D, Morawetz C, Heekeren HR. 2013. Nucleus accumbens response to gains in reputation for the self relative to gains for others predicts social media use. *Front Hum Neurosci* 7:1–11.
- Middleton F, Strick P. 2000a. Basal ganglia and cerebellar loops: motor and cognitive circuits. *Brain Res Brain Res Rev* 31:236–50.
- Middleton F, Strick P. 2000b. Basal ganglia output and cognition: evidence from anatomical, behavioral, and clinical studies. *Brain Cogn* 42:183–200.
- Mobbs D, Yu R, Meyer M, Passamonti L, Seymour B, Calder AJ, and others. 2009. A key role for similarity in vicarious reward. *Science* 324:900.
- Niv Y. 2009. Reinforcement learning in the brain. *J Math Psychol* 53:139–54.
- Niv Y, Schoenbaum G. 2008. Dialogues on prediction errors. *Trends Cogn Sci* 12:265–72.
- O'Doherty J, Dayan P, Schultz J, Deichmann R, Friston K, Dolan R. 2004. Dissociable roles of ventral and dorsal striatum in instrumental conditioning. *Science* 304:452–4.
- O'Doherty J, Kringelbach ML, Rolls ET, Hornak J, Andrews C. 2001. Abstract reward and punishment representations in the human orbitofrontal cortex. *Nat Neurosci* 4:95–102.
- O'Doherty J, Winston J, Critchley H, Perrett D, Burt DM, Dolan RJ. 2003b. Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia* 41:147–55.
- O'Doherty JP. 2004. Reward representations and reward-related learning in the human brain: insights from neuroimaging. *Curr Opin Neurobiol* 14:769–76.
- O'Doherty JP, Buchanan TW, Seymour B, Dolan RJ. 2006. Predictive neural coding of reward preference involves dissociable responses in human ventral midbrain and ventral striatum. *Neuron* 49:157–66.
- O'Doherty JP, Dayan P, Friston K, Critchley H, Dolan RJ. 2003a. Temporal difference models and reward-related learning in the human brain. *Neuron* 38:329–37.
- O'Doherty JP, Deichmann R, Critchley HD, Dolan RJ. 2002. Neural responses during anticipation of a primary taste reward. *Neuron* 33:815–26.
- Ostlund SB, Balleine BW. 2005. Lesions of medial prefrontal cortex disrupt the acquisition but not the expression of goal-directed learning. *J Neurosci* 25:7763–70.
- Ostlund SB, Balleine BW. 2007. The contribution of orbitofrontal cortex to action selection. *Ann N Y Acad Sci* 1121:174–92.
- Packard MG, Knowlton BJ. 2002. Learning and memory functions of the basal ganglia. *Annu Rev Neurosci* 25:563–93.
- Palminteri S, Justo D, Jauffret C, Pavlicek B, Dauta A, Delmaire C, and others. 2012. Critical roles for anterior insula and dorsal striatum in punishment-based avoidance learning. *Neuron* 76:998–1009.
- Pennartz CMA, Ito R, Verschure PFMJ, Battaglia FP, Robbins TW. 2011. The hippocampal striatal axis in learning, prediction and goal-directed behavior. *Trends Neurosci* 34:548–59.
- Pessiglione M, Seymour B, Flandin G, Dolan R, Frith C. 2006. Dopamine-dependent prediction errors underpin reward-seeking behaviour in humans. *Nature* 442:1042–5.
- Phan KL, Sripada CS, Angstadt M, McCabe K. 2010. Reputation for reciprocity engages the brain reward center. *Proc Natl Acad Sci U S A* 107:13099–104.
- Plassmann H, O'Doherty J, Rangel A. 2007. Orbitofrontal cortex encodes willingness to pay in everyday economic transactions. *J Neurosci* 27:9984–8.
- Rademacher L, Krach S, Kohls G, Irmak A, Gründer G, Spreckelmeyer KN. 2010. Dissociation of neural networks for anticipation and consumption of monetary and social rewards. *Neuroimage* 49:3276–85.
- Rand DG, Arbesman S, Christakis NA. 2011. Dynamic social networks promote cooperation in experiments with humans. *Proc Natl Acad Sci U S A* 108:19193–8.
- Rand DG, Greene JD, Nowak MA. 2012. Spontaneous giving and calculated greed. *Nature* 489:427–30.
- Rapoport A, Chammah AM. 1965. Prisoner's dilemma: a study in conflict and cooperation. Ann Arbor, MI: University of Michigan Press.
- Rescorla R, Wagner A. 1972. A theory of Pavlovian conditioning: variations in the effectiveness of reinforcement and non-reinforcement. In: Black AH, Prokasy WF, editors. *Classical conditioning II: current theory and research*. New York, NY: Appleton-Century-Crofts. p 64–99.
- Rilling J, Gutman D, Zeh T, Pagnoni G, Berns G, Kilts C. 2002. A neural basis for social cooperation. *Neuron* 35:395–405.
- Rilling JK, Sanfey AG. 2011. The neuroscience of social decision-making. *Annu Rev Psychol* 62:23–48.
- Rilling JK, Sanfey AG, Aronson JA, Nystrom LE, Cohen JD. 2004. Opposing BOLD responses to reciprocated and unreciprocated altruism in putative reward pathways. *Neuroreport* 15:2539–43.
- Robbins T, Everitt B. 1996. Neurobehavioural mechanisms of reward and motivation. *Curr Opin Neurobiol* 6:228–36.
- Robbins TW, Cador M, Taylor JR, Everitt BJ. 1989. Limbic-striatal interactions in reward-related processes. *Neurosci Biobehav Rev* 13:155–62.

- Schonberg T, Daw N, Joel D, O'Doherty J. 2007. Reinforcement learning signals in the human striatum distinguish learners from nonlearners during reward-based decision making. *J Neurosci* 27:12860–7.
- Schultz W. 1997. Dopamine neurons and their role in reward mechanisms. *Curr Opin Neurobiol* 7:191–7.
- Schultz W, Dayan P, Montague P. 1997. A neural substrate of prediction and reward. *Science* 275:1593–9.
- Sesack SR, Grace AA. 2010. Cortico-basal ganglia reward network: microcircuitry. *Neuropsychopharmacology* 35:27–47.
- Shohamy D. 2011. Learning and motivation in the human striatum. *Curr Opin Neurobiol* 21:408–14.
- Shohamy D, Adcock RA. 2010. Dopamine and adaptive memory. *Trends Cogn Sci* 14:464–72.
- Smith DV, Hayden BY, Truong T-K, Song AW, Platt ML, Huettel SA. 2010. Distinct value signals in anterior and posterior ventromedial prefrontal cortex. *J Neurosci* 30:2490–5.
- Somerville LH, Heatherton TF, Kelley WM. 2006. Anterior cingulate cortex responds differentially to expectancy violation and social rejection. *Nat Neurosci* 9:1007–8.
- Somerville LH, Kelley WM, Heatherton TF. 2010. Self-esteem modulates medial prefrontal cortical responses to evaluative social feedback. *Cereb Cortex* 20:3005–13.
- Steinberg L. 2008. A social neuroscience perspective on adolescent risk-taking. *Dev Rev* 28:78–106.
- Sutton RS, Barto AG. 1998. Reinforcement learning: an introduction. Cambridge, MA: MIT Press.
- Tricomi E, Delgado MR, Fiez JA. 2004. Modulation of caudate activity by action contingency. *Neuron* 41:281–92.
- Tricomi E, Delgado MR, McCandliss BD, McClelland JL, Fiez JA. 2006. Performance feedback drives caudate activation in a phonological learning task. *J Cogn Neurosci* 18:1029–43.
- Tricomi E, Fiez JA. 2008. Feedback signals in the caudate reflect goal achievement on a declarative memory task. *Neuroimage* 41:1154–67.
- van Winden F, Stallen M, Ridderinkhof R. 2008. On the nature, modeling and neural bases of social ties. In: Houser D, McCabe K, editors. *Neuroeconomics*. Bingley, UK: JAI Press. p 125–60.
- Voorn P, Vanderschuren LJ, Groenewegen HJ, Robbins TW, Pennartz CM. 2004. Putting a spin on the dorsal-ventral divide of the striatum. *Trends Neurosci* 27:468–74.
- Vrtička P, Vuilleumier P. 2012. Neuroscience of human social interactions and adult attachment style. *Front Hum Neurosci* 6:212.
- Williams K, Cheung C, Choi W. 2000. Cyberostracism: effects of being ignored over the Internet. *J Pers Soc Psychol* 79:748–62.
- Yarkoni T, Poldrack RA, Nichols TE, Van Essen DC, Wager TD. 2011. Large-scale automated synthesis of human functional neuroimaging data. *Nat Methods* 8:665–70.
- Zink CF, Pagnoni G, Martin-Skurski ME, Chappelow JC, Berns GS. 2004. Human striatal responses to monetary reward depend on saliency. *Neuron* 42:509–17.